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Restoration of Herbaceous Woodland Plants: Persistence, Growth, and Reproductive Success of Local and Non-local Propagules

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Abstract
Restoring the forest herbaceous layer in remnant forests throughout the Midwestern United States (U.S.) is limited by the lack of seed and propagules for many plant species. As a result, restorationists often have limited material to work with and must seek out plant material at a regional rather than a local scale, without knowing whether regional provenances are ecologically appropriate. We conducted greenhouse and field experiments to examine persistence, growth, and reproduction of three herbaceous perennials (wild ginger, Virginia waterleaf, and James' sedge) that could be used for restoration. The greenhouse experiment represented a common garden and was conducted to identify whether there were genetic differences in morphological characters between local plants and non-local transplants from commercial nurseries. The two-year field study was conducted to determine whether any genetic differences noted in the greenhouse persisted in a natural setting, and also to determine what planting density (two or five individuals in a 0.25 m^2 plot) would be sufficient for the plants to establish. In the greenhouse, growth and reproductive measures for non-local plants were generally equal to or greater than those of local plants. However, we found the reverse for many traits, particularly related to reproduction, in the field during year two. In natural field conditions local plants had equal or greater vegetative growth and reproduction than non-local plants, although both had similar persistence. Further, similar persistence and growth in low- and high-density field plots suggested that a limited number of transplants would be adequate for successful establishment of non-local transplant stock.

Keywords
common garden, hardwood forests, reintroduction, transplantation

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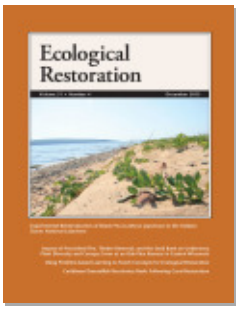

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RESEARCH ARTICLE

Restoration of Herbaceous Woodland Plants: Persistence, Growth, and Reproductive Success of Local and Non-local Propagules

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ABSTRACT

Restoring the forest herbaceous layer in remnant forests throughout the Midwestern United States (U.S.) is limited by the lack of seed and propagules for many plant species. As a result, restorationists often have limited material to work with and must seek out plant material at a regional rather than a local scale, without knowing whether regional provenances are ecologically appropriate. We conducted greenhouse and field experiments to examine persistence, growth, and reproduction of three herbaceous perennials (wild ginger, Virginia waterleaf, and James' sedge) that could be used for restoration. The greenhouse experiment represented a common garden and was conducted to identify whether there were genetic differences in morphological characters between local plants and non-local transplants from commercial nurseries. The two-year field study was conducted to determine whether any genetic differences noted in the greenhouse persisted in a natural setting, and also to determine what planting density (two or five individuals in a 0.25 m² plot) would be sufficient for the plants to establish. In the greenhouse, growth and reproductive measures for non-local plants were generally equal to or greater than those of local plants. However, we found the reverse for many traits, particularly related to reproduction, in the field during year two. In natural field conditions local plants had equal or greater vegetative growth and reproduction than non-local plants, although both had similar persistence. Further, similar persistence and growth in low- and high-density field plots suggested that a limited number of transplants would be adequate for successful establishment of non-local transplant stock.

Keywords: common garden, hardwood forests, reintroduction, transplantation

Land use change, including agricultural and urban intensification, has accelerated in the Midwest in recent decades. As greater land use pressure and diminishing area of intact ecosystems become the norm (Secchi et al. 2008), restoring and maximizing function in remnant natural systems is of increasing importance. In Iowa particularly, remnant forests are small and often associated with small streams and waterways (Thompson 1992, Moser 2009). These areas are critical for conservation because they perform numerous functions, including coupling terrestrial and aquatic systems in water and nutrient storage and cycling (Gomi et al. 2002), curtailing soil erosion (Hunsaker and Neary 2012), protecting biodiversity, and maintaining attractive areas for public and private recreation (Moser et al. 2009). However, there is evidence that remnant forests have diminished capacity to provide these ecosystem services, (Groffman et al. 2003, Bernhardt et al. 2008) and may require restoration efforts to maintain or re-create these ecosystem functions.

The herbaceous layer is an important, but sometimes overlooked component of these forests. Recent research in central Iowa indicates that herbaceous plant species composition shifts from forest specialists to weedy and exotic generalists in highly disturbed areas such as urban or grazed forests (Gerken Golay et al. 2013, Mabry et al. 2008). In addition, water quality is degraded in streams within these forests in part because fewer nutrients may be captured by the vegetation, particularly in early spring and late fall (Gerken et al. 2013). Some herbaceous species, especially forest specialists or those requiring forest interiors, may be reduced in number or completely absent in degraded forests (Robinson et al. 1994, Groffman et al. 2003), leaving their role unfilled for nutrient capture, biodiversity, and aesthetics (Bormann et al. 1968, Drayton and Primack 1996, Gilliam 2007).

Two main challenges commonly arise on the topic of restoration plantings. The first challenge is to determine the appropriate collection zone for seeds and transplants (Hufford and

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Mazer 2003, McKay et al. 2005). The operation of succession at small scales, which can result in local adaptation, has been summarized for many species in a review that has become an often-cited basis for concern about locally-adapted ecotypes (Linhart and Grant 2006). However, little is known about the genetics of species that could be useful for herbaceous layer restoration (McKay et al. 2005), including early-flowering perennials and sedges (Whigham 2004).

At a minimum, to demonstrate local adaptation, genetic variation among populations needs to be established. Common garden studies are the classic method of determining whether this variation exists (Hufford and Mazer 2003). Further, differences observed in common gardens must then be expressed under field conditions, and under these conditions local plants must demonstrate greater persistence and reproductive fitness compared to non-local plants, consistently over both time and variation in environmental conditions (Bazzaz and Sultan 1987).

The second challenge is related to the exacting germination, seed storage requirements, and slow growth from seed that are characteristic of many woodland herbaceous species, making transplants a more feasible way to restore these populations (Bierzychudek 1982, Mottl et al. 2006). Here, an important issue is to identify what minimum density of transplants is sufficient to ensure persistence. Although there is some research on restoration protocols for woodland perennials (e.g. Mottl et al. 2006, Drayton and Primack 2012), there is little information on the planting densities needed for persistence and recruitment of forest herbaceous species. Field comparisons of high- and low-density plantings could offer insight on comparative establishment rates, and tie these rates to the potential costs involved.

In this study, we sought to address two practical questions: 1) Do plants that are commercially available in the region show evidence of among-population genetic variation, phenotypic plasticity, or both? and 2) Is low density planting sufficient to establish new populations? We approached these questions by comparing local and non-local plants (individuals from two different regional populations) of two forest herbaceous species in a common-garden greenhouse experiment and in a field experiment, and by comparing high- and low-density plantings of non-local transplants in the field experiment.

Materials and Methods

Species selection and propagule sources

Our goal was to examine restoration potential of species that are desirable for both ecological and aesthetic reasons. We chose two species, wild ginger (*Asarum canadense*, hereafter ginger) and Virginia waterleaf (*Hydrophyllum virginianum*, hereafter waterleaf) for their persistence, flowering, and abundant vegetative spread once established (Mottl et al. 2006). In contrast, seed production by both species is limited; they have exacting seed storage requirements and are slow to germinate (Cullina 2000). We used ginger and waterleaf in both the field and greenhouse studies, and included a third species, James' sedge (*Carex jamesii*, hereafter sedge) in the field study only. This sedge was chosen to represent graminoids and because it is similar to ginger and waterleaf with respect to seed-versus-transplant potential. In addition, all three species are good candidates for herbaceous layer restoration (based on personal observation) because they are 1) common in relatively undisturbed forests of the region, 2) commercially available in the Midwest, 3) easy to distinguish from related species (e.g. other sedges) 4) attractive, 5) less susceptible to deer herbivory, and 6) native forest perennials that require virtually no maintenance once established, and may therefore be more cost-effective over the long-term. These additional criteria were included to increase the likelihood that landowners and land managers would purchase and plant these species if we could document successful establishment.

Non-local transplants were obtained from the nearest available commercial source of stock. Ginger and waterleaf were obtained from Prairie Moon Nursery, Winona, MN, approximately 400 km from the planting sites. These plants were collected from natural forest populations, cold-stored, and shipped as bare-root stock in aerated plastic sacks packed in planting mixture (in October 2010 for the field planting, and in March 2012 for the greenhouse study). Non-local transplants of sedge were obtained from Spence Restoration Nursery, Muncie, IN, approximately 840 km distant. These plants were obtained from divisions made in May 2010 and grown outdoors in an unheated cold frame under a shade tarp. Because stems and leaves of this sedge do not annually senesce as completely as ginger and waterleaf, sedges were shipped as potted plants in 6 cm square by 9.5 cm deep pots in early October 2010. Non-local sedge was not available commercially at the time of the greenhouse experiment, so it could not be included. Local plants of ginger and waterleaf for the greenhouse study were collected after first leaves emerged (on March 12, 2012) from a minimally disturbed central Iowa forest near Nevada, IA, within 60 km of the field planting sites.

Greenhouse Study

Planting Methods. Both local and non-local ginger and waterleaf were cold-stored upon receiving them and potted within two days. Twenty five individuals of each species from both local and non-local populations were potted in 15.2 cm round pots using Sunshine LC1 Mix growing medium, for a total of 50 plants per species. We watered all plants at the time of potting and arranged pots in a grid of 5

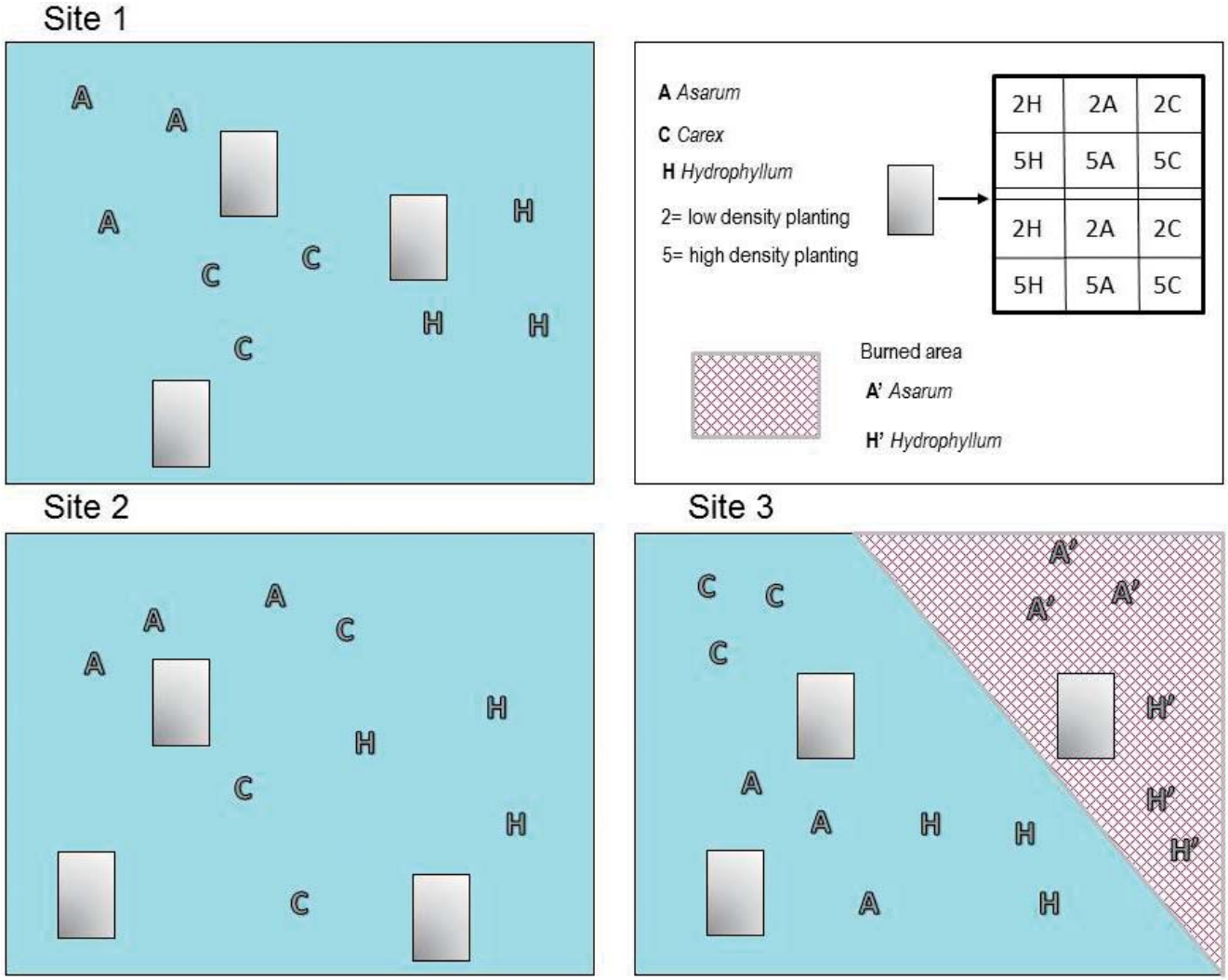

Figure 1. Schematic plot design for restoration study in Des Moines area parks. At each of the three forested park sites, three plots with 12 quadrats and three reference plants of each species were established. Alphabetic characters outside of the gray planting plots denote locations of reference plants at each site. A portion of Site 3 was burned after planting, so additional reference plants were identified for comparison to affected species.

pots per column and 10 per row, alternating between local and non-local plants. Plant care was uniform across species and sources, and all plants were partially shaded by a row of trees present in the same greenhouse bay.

Data Collection and Analysis. We monitored plant development in April and May, 2012. For both species, we assessed vegetative growth and reproductive traits including leaf number, petiole diameter, flower number, fruit number, and number of seeds per fruit. For ginger, we also measured leaf length and width (and estimated leaf area as width multiplied by length). For waterleaf, we also measured height of the tallest leaf. Ginger measurements were taken on April 18, and waterleaf measurements were taken on April 30. We harvested fruit on May 27th, including all available fruit on ginger, and 3 fruits from each plant for waterleaf. We then air dried and dissected fruits to record seed count. We took all measurements manually by counting, or using a ruler or digital calipers.

To analyze differences between local and non-local plants, we conducted a one-way Analysis of Variance (ANOVA) (JMP 9.0; SAS Institute, Cary, NC). We grouped data by source population location (independent variable) and analyzed vegetative growth and reproductive traits individually as response variables. We set our p-value at 0.05.

Field Study

Study Sites. We conducted the field study in three parks in the Des Moines Parks and Recreation system in central Iowa. We selected these urban parks according to the following criteria: the forests were mature oak-hickory communities on uplands and slopes under the same land use, there was no harvest or other alteration to the stand for 30 years or more, and all were under the same urban park forest management plan (Julie Hempel, Des Moines Parks and Recreation, pers. comm.). Forested areas in these parks ranged from 8 to 17 ha. We placed three plots

in each park for a total of nine plots. Plots experienced no active management during the survey period, with the exception of one plot that was unintentionally included as part of a controlled burn in early spring 2011. We spaced planting plots a minimum of 50 m apart, an order of magnitude farther than the mean distance for ant-dispersal typical of these species (Bierzychudek 1982). For this reason, we considered all nine plots independent and used site as a blocking factor.

Planting Methods. Nursery stock of ginger, waterleaf, and sedge were cold-stored for less than one week before planting. Because sparse populations of each of these species were found in all three forests, plot preparation involved removing all previously existing plant material (roots and shoots) by hand. We installed plants, and applied sawdust mulch and water. We watered all plants again within a week. Precipitation was sufficient in fall 2010 so we provided no additional watering.

We divided each restoration plot in half with each half separated by a 0.5 m walkway to allow access to the plants (Figure 1). We then subdivided each half-plot into six 0.25 m^2 quadrats and randomly assigned each a planting treatment. Within each quadrat, we planted only one species. This planting design resulted in two subsamples each of ginger, waterleaf, and sedge at high density (five individuals, representing natural density for these plants), and two subsamples each at low density (two individuals) for a total of 18 quadrats per species/density combination (Figure 1). We averaged subsample data and used plots as the sampling unit for statistical analysis.

At each forest site we identified a minimum of three naturally-occurring local reference plants of the target species that approximate the size and leaf number of the transplanted stock, using these as a proxy for age. We flagged individual reference plants that occurred at least five meters away from the planted plots. To account for the controlled burn, we also included reference plants of ginger and waterleaf that occurred in the burn zone (sedge did not naturally occur in the burn zone). We were unable to relocate a total of five of the local reference plants in 2012 because flags had been removed. In these instances, we identified new reference plants.

Data Collection and Analysis. Based on our knowledge of phenology, we surveyed plots from April 12 to May 24, 2011 (year one) and May 10 to June 16, 2012 (year two) to measure persistence, growth, and reproduction. We measured persistence by documenting presence/absence of transplants in each quadrat. Growth and reproductive measurements for ginger and waterleaf were measured in the same manner as for the greenhouse study, with measurements made on each plant individually and averaged for the quadrat. Subsamples (quadrats) were averaged for each plot (n = 9 for low density and n = 9 for high density). Local plant measurements were taken on individual reference plants and averaged for each site (n = 3 for sedge and n = 4 for ginger and waterleaf, because burned reference plants were included).

For sedge, we counted number of flowers, fruits, and leaves. For our purposes, a sedge perigynium was defined as a "fruit" and a "leaf" was defined as a combination leaf/stem, which usually contained three leaf blades. We took measurements in the field on one date per species within the time frame specified above. After flowering, we harvested fruit of ginger and waterleaf, dried, and dissected them, as in the greenhouse study. Sedge perigynia consist of only one achene, and so we obtained fruit counts directly.

We compared persistence by determining the proportion of quadrats for each density/species combination with surviving transplants. Recruitment was estimated as the proportion of quadrats with more individuals than were originally planted. We compared plant growth and reproductive traits using two separate one-way ANOVAs with planting type (local reference plants versus high density non-local plants) and density (high versus low for non-local plants) as the predictor variables and measurements of growth and reproductive traits as the response variables. Data exhibited a normal distribution, factors were treated as fixed, and no transformations were made. We set our accepted *p*-value at 0.05.

Results

Greenhouse planting

Non-local ginger plants had greater leaf area, petiole diameter, and flower number than local plants (Table 1). There was also a trend toward greater fruit number, although this was not detectable statistically. Trait measures for non-local waterleaf plants were also greater than local plants (except for leaf number) although these could not be detected statistically due to high standard deviations, with the exception of petiole diameter which was significantly larger for non-local plants (Table 1). All plants persisted beyond the duration of the greenhouse study.

Field planting

Persistence, measured at the quadrat level, was high both years for all three species and at both densities. In year one, ginger had 94% or greater persistence, and waterleaf and sedge had 100% persistence (Table 2). In year two, ginger had between 83% (low density) and 89% (high density) persistence, while waterleaf and sedge had 94% (low density) to 100% (high density) persistence. Recruitment of new individuals via clonal spread or germination in year two occurred for ginger and waterleaf at low densities, and for all three species at high densities (Table 2).

There were few differences in mean vegetative and reproductive metrics for local versus non-local plants (based on high-density plots) in the field during year one (Table 3). For ginger, non-local plants had greater petiole

Table 1. Vegetative and reproductive trait means for local (Iowa) and non-local (Minnesota) wild ginger and Virginia waterleaf plants grown in a common-garden greenhouse setting at Iowa State University, Ames, IA.

	Local	Non-local	df	Mean square	F	*p*
Wild ginger						
Leaf number	3.8	3.8	1	0.1	0.04	0.8389
Error			48	1.9		
Leaf area (cm)	26.67	51.28	1	7571.0	30.94	<0.0001
Error			48	244.7		
Petiole dia. (mm)	2.20	3.51	1	21.4	193.81	<0.0001
Error			48	0.1		
Flower number	0.8	1.4	1	3.9	7.92	0.0071
Error			48	0.5		
Fruit number	0.7	1.0	1	1.6	3.81	0.0567
Error			48	0.4		
Seeds per fruit	37.2	32.0	1	241.8	3.41	0.0735
Error			34	70.9		
Virginia waterleaf						
Height of tallest leaf	11.84	13.39	1	30.1	3.98	0.0516
Error			48	7.6		
Leaf number	10.1	8.2	1	42.3	2.53	0.1186
Error			48	16.8		
Petiole dia.(mm)	3.03	3.71	1	5.6	8.82	0.0046
Error			48	0.6		
Flower number	23.2	30.8	1	729.6	0.72	0.4019
Error			48	1020.3		
Fruit number	10.8	14.0	1	134.5	0.52	0.4746
Error			48	258.9		
Seeds per fruit	2.3	2.7	1	0.9	0.79	0.3829
Error			24	1.1		

diameter, whereas local plants had a greater number of seeds per fruit in year one. There were no differences between local and non-local plants for waterleaf or sedge in year one. In year two, local ginger had an order of magnitude more flowers and fruits than the non-local plants, and three times the number of seeds per fruit. Local waterleaf had greater height of the tallest leaf, and many more seeds per fruit than non-local plants. There were again no differences between local and non-local sedge in year two (Table 3).

In the comparison of planting densities, high density ginger had two times as many leaves as low density, and low density sedge had twice the number of leaves as high density, during year one (Table 4). There were no differences for any species or traits in year two (Table 4).

Discussion

This relatively small-scale study suggests that more field trials are needed to fully understand how population variation observed in common garden settings translates into variation in natural settings and over time as environmental conditions change. If local plants consistently outperform non-local plants across the full range of environmental conditions that these plants encounter, then we can conclude that local plants are more suitable for restoration plantings. Further, low-density plantings (two plants) appear to be as effective as high-density plantings (five plants) in terms of persistence, vegetative growth, reproductive traits, and recruitment over two years, thus pointing to a way to reduce the cost of restoration.

The greenhouse portion of this study demonstrated that genetic differences exist between local and non-local populations of ginger and waterleaf for some traits. Non-local plants were the same as or more robust than local transplants in the greenhouse, with respect to both vegetative and reproductive traits. This common-garden approach is the classic

Table 2. Persistence and recruitment of non-local wild ginger, Virginia waterleaf, and James' sedge transplants grown in field restoration plots at high- and low-density in Des Moines, IA.

		% Persistence		% Recruitment
	Density	Year 1	Year 2	Year 2
Wild ginger	Low	94.4	83.3	38.9
	High	100.0	88.9	16.7
Virginia waterleaf	Low	100.0	94.4	50.0
	High	100.0	100.0	11.1
James' sedge	Low	100.0	94.4	0.0
	High	100.0	100.0	5.6

Table 3. Vegetative and reproductive metrics compared between local and non-local wild ginger, Virginia waterleaf, and James' sedge in Des Moines, IA forest research sites.

Metric	Field Year 1						Field Year 2					
	Local ref.	Non-local high density	df	Mean square	F	*p*	Local ref.	Non-local high density	df	Mean square	F	*p*
Wild ginger												
Leaf number	3.3	2.5	1	0.9	3.24	0.1317	4.6	1.6	1	13.8	3.56	0.1324
Error			5	0.3					4	3.9		
Leaf area (cm)	20.30	27.72	1	94.19	0.72	0.4363	24.24	21.67	1	11.30	0.03	0.8655
Error			5	131.71					5	355.52		
Petiole diameter (mm)	2.225	3.099	1	1.312	17.63	0.0085	2.058	1.911	1	0.033	0.07	0.8032
Error			5	0.074					4	0.461		
Flower number	0.4	0.8	1	0.2	3.52	0.1195	1.1	0.1	1	1.4	1.40	0.3024
Error			5	0.1					4	1.0		
Fruit number	0.4	0.5	1	0.0	0.59	0.4782	1.1	0.1	1	1.6	192.19	<0.0001
Error			5	0.0					5	0.0		
Seeds per fruit	19.0	4.0	1	383.3	22.46	0.0052	25.5	7.7	1	541.0	16.57	0.0096
Error			5	17.1					5	32.7		
Virginia Waterleaf												
Height of tallest leaf (cm)	19.38	14.43	1	42.08	2.83	0.1533	18.34	12.45	1	59.44	199.11	<0.0001
Error			5	14.87					5	0.30		
Leaf number	7.3	5.2	1	7.3	4.57	0.0856	3.3	2.4	1	1.3	0.89	0.3876
Error			5	1.6					5	1.5		
Petiole diameter (mm)	3.521	2.886	1	0.691	4.06	0.1001	2.560	2.220	1	0.198	3.27	0.1302
Error			5	0.170					5	0.061		
Flower number	22.9	18.1	1	39.7	0.41	0.5487	7.2	4.0	1	17.8	0.89	0.3882
Error			5	96.1					5	20.0		
Fruit number	3.7	4.4	1	0.8	0.10	0.7616	3.7	0.3	1	20.2	2.72	0.1599
Error			5	7.5					5	7.4		
Seeds per fruit	2.7	0.8	1	5.8	12.56	0.0239	2.7	0.1	1	10.7	23.51	0.0083
Error			4	0.5					4	0.5		
James' sedge												
Leaf number	34.4	3.4	1	1446.1	2.31	0.2035	20.0	24.2	1	26.4	0.11	0.7618
Error			4	627.2					4	250.6		
Flower number	13.6	7.6	1	52.4	0.71	0.4464	1.9	5.9	1	24.5	4.51	0.1009
Error			4	73.7					4	5.4		
Fruit number	26.4	10.0	1	405.0	1.42	0.2990	3.1	8.3	1	39.7	2.23	0.2100
Error			4	284.9					4	17.8		

method of determining whether there is genetic variation within species (Hufford and Mazer 2003), but it does not reveal whether this variation is ecologically meaningful in the field (Miner et al. 2005). Particularly for wild ginger, the field planting portion of this study indicates that these genetic differences do not necessarily translate into field-expressed advantages in all years. In a dry year, the non-local plants of ginger and waterleaf were less robust than local plants in the field, particularly in fitness-related traits. Thus, while the greenhouse experiment demonstrated that genetic differences exist, the difference in performance between greenhouse and field demonstrates that ginger and waterleaf are also capable of plastic response to environmental variation.

The fact that we observed both genetic differences among the two populations and plastic response to varying environment is not surprising. It is common that genetic variation observed under controlled conditions changes or disappears under natural field conditions (Bazzaz and Sultan 1987, Miner et al. 2005). The two modes are sometimes seen as opposing ways of dealing with environmental variation, but in fact, may be complementary (Joshi et al. 2001). Other studies have also found that both processes are often in play (Stanton 1984, Maddox and Root 1987, Joshi et al. 2001, Seliskar et al. 2002, Bossdorf et al. 2005).

Table 4. Vegetative and reproductive metrics compared for high versus low density of wild ginger, Virginia waterleaf, and James' sedge transplants grown in Des Moines, IA forest herbaceous plant restoration plots.

Metric	Field Year 1						Field Year 2					
	Non-local high density	Non-local low density	df	Mean square	F	*p*	Non-local high density	Non-local low density	df	Mean square	F	*p*
Wild ginger												
Leaf number	2.5	2.5	1	0.0	0.00	0.9602	1.6	1.5	1	0.0	0.05	0.8270
Error			16	0.4					16	0.6		
Leaf area (cm)	27.72	22.81	1	108.23	2.18	0.1591	21.67	21.13	1	1.30	0.00	0.9577
Error			16	49.61					16	447.23		
Petiole diameter (mm)	3.099	2.902	1	0.175	0.73	0.4041	1.911	1.820	1	0.037	0.04	0.8507
Error			16	0.239					16	1.013		
Flower number	0.8	0.4	1	0.7	11.38	0.0039	0.1	0.1	1	0.0	0.00	1.0000
Error			16	0.1					16	0.0		
Fruit number	0.5	0.3	1	0.2	3.07	0.0987	0.1	0.1	1	0.0	0.00	1.0000
Error			16	0.1					16	0.0		
Seeds per fruit	4.0	3.1	1	4.1	0.73	0.4062	7.7	7.7	1	0.0	0.00	1.0000
Error			15	5.6					16	85.4		
Virginia waterleaf												
Height of tallest leaf (cm)	14.43	14.40	1	0.00	0.00	0.9819	12.45	13.04	1	1.54	0.40	0.5378
Error			16	8.12					16	3.89		
Leaf number	5.2	5.9	1	2.1	1.31	0.2685	2.4	2.6	1	0.2	0.18	0.6795
Error			16	1.6					16	0.9		
Petiole diameter (mm)	2.886	3.035	1	0.100	0.46	0.5069	2.220	2.162	1	0.015	0.09	0.7711
Error			16	0.216					16	0.172		
Flower number	18.1	28.4	1	482.3	1.25	0.2798	4.0	1.5	1	26.8	1.46	0.2438
Error			16	385.4					16	18.3		
Fruit number	4.4	4.4	1	0.0	0.00	0.9551	0.3	0.6	1	0.6	0.48	0.5004
Error			16	10.4					16	1.2		
Seeds per fruit	0.8	0.8	1	0.0	0.00	0.9789	0.1	0.3	1	0.3	1.41	0.2526
Error			16	0.3					16	0.2		
James' sedge												
Leaf number	3.4	6.8	1	53.5	11.90	0.0033	24.2	26.5	1	24.5	0.16	0.6975
Error			16	4.5					16	156.5		
Flower number	7.6	7.8	1	0.1	0.00	0.9606	5.9	8.3	1	25.7	0.70	0.4136
Error			16	24.0					16	36.4		
Fruit number	10.0	10.5	1	1.0	0.01	0.9089	8.3	11.2	1	37.9	0.48	0.4985
Error			16	73.3					16	79.0		

The better performance of local plants may have been due to challenging conditions in the field during the second year when the study area, Des Moines, Iowa, had 11.6 cm less precipitation from January–June than the same interval in year one (Iowa Environmental Mesonet 2012). In fact, the state was 22 cm below the normal average for the preceding 12 months, while temperatures were 2.6°C higher than average in year two [National Climatic Data Center (NCDC) 2012]. The non-local plants of ginger and waterleaf were from southern Minnesota, an area with typically cooler conditions than central Iowa (normal annual mean temperature 9.4°C versus 10°C, respectively; NCDC 2012). Thus, this study provides some evidence that Minnesota as a source population needs further investigation as a choice for Iowa plantings, particularly given occasional but recurring drought conditions.

There is an important caveat to concluding that non-local plants are unsuitable overall and one that pertains to conclusions about local adaptation generally. In order to definitively conclude, in this case for example, that the Minnesota plants are unsuitable for restoration in Iowa, it would be necessary to show that they are consistently less persistent or less fit compared to local plants across all the environmental conditions encountered over time (Sultan

1987). The difference we observed between greenhouse and field for Minnesota and Iowa plants was due to phenotypic plasticity, the ability of different genotypes to express different phenotypes as the environment changes (Bazzaz and Sultan 1987, Sultan 1987). For example, in this case if Minnesota plants outperform Iowa plants in seasons that are cool and moist, we can only conclude that we are observing morphological characters that are continuing to change plastically in response to weather. However, if Iowa plants consistently outperform Minnesota plants across the variety of weather conditions these long-lived plants encounter, then we can conclude that there is a genetic basis to the response and that the Minnesota provenance for these species is not the best choice for use in Iowa.

In other words, conclusions about whether we observed local adaptation or phenotypic plasticity cannot be answered without long-term monitoring. In fact, continuous monitoring of restoration projects is frequently noted as the most feasible option for determining appropriate collection zones (Millar and Libby 1989, Rice and Emery 2003, McKay et al. 2005, Saari and Glisson 2012). This points to the importance of documenting sources of seeds and transplants as well as precise location of individual plants at restoration sites, and conducting long-term monitoring of their survival and growth (Millar and Libby 1989, Saari and Glisson 2012). It would also be very useful to match these data to variation in life history traits and influence of gene flow in order to determine how collection zones vary with potential gene flow, and to determine if there are generalizable correlations between gene flow potential due to these traits and genetic differentiation (Loveless and Hamrick 1984).

A second caveat is that the reference plants we chose in the field were not subjected to transplant stress. If local plants demonstrated greater persistence or vegetative growth than non-local plants in the first year when conditions were ideal, we would have concluded that this omission confounded our results. Instead, the transplanted non-local plants were generally equal to or in some cases larger than local plants in year one, with the exception of seeds per fruit. This suggests that any stress from transplantation was insufficient to cause non-local plants to be inferior to local plants. Ginger and waterleaf are robust plants that can begin spreading within one season (Mottl et al. 2006); thus any transplant stress would not be likely to persist into the second season.

At the same time, we documented excellent persistence rates for all of the non-local plants in the field experiment, and evidence of recruitment for non-local plants of all three species at both densities. Although we monitored for only two years, other researchers and practitioners have documented longer-term survival of similar transplants (e.g. seven years for ginger and waterleaf, Mottl et al. 2006). In addition, recruitment of new individuals within the two-year time frame of this study for all three species is very encouraging. Our persistence and recruitment data suggest that low-density plantings using transplants for forest understory restoration are feasible, likely to be successful, and an economically viable approach for restoration practitioners even when budget limitations exist.

In conclusion, given historical human impacts on forest composition and new pressures on the forest remnants that exist in the Midwestern landscape, restoration of understory species that are likely to contribute to enhanced ecological functions (for biodiversity, water quality, and aesthetic purposes) should be of increasing interest. The species we chose to study are among those that are likely to provide benefits for all three purposes (e.g. Mabry et al. 2008, Gerken et al. 2010). Our next step in this work is to expand the comparative framework (Richards et al. 2006) to include more species grown under controlled conditions compared to field conditions, and to include a rigorous test of field-based performance for Iowa plants compared to non-local plants.

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